REVIEW

Control of root system architecture by phytohormones and environmental signals in rice

Chen Lin and Margret Sauter

Plant Developmental Biology and Plant Physiology, University of Kiel, Am Botanischen Garten 5, 24118 Kiel, Germany

ABSTRACT

Drought and flooding are environmental extremes and major threats to crop production. Water uptake is achieved by plant roots which have to explore new soil spaces to alleviate water deficit during drought or to cope with water excess during flooding. Adaptation of the root system architecture helps plants cope with such extreme conditions and is crucial for plant health and survival. While for dicot plants the well studied model plant *Arabidopsis thaliana* has provided insight into the genetic and molecular regulation of the root system, less information is available for monocot species, which include the agronomically important cereal crops. Rice (*Oryza sativa* L.) is a semi-aquatic monocot plant that develops strong tolerance to flooding. Flooding tolerance of rice is closely linked to its adaptive root system. The functional root system of rice is mainly composed of crown roots and is shifted to nodal adventitious roots during flooding which allows rice to maintain oxygen supply to the roots and to survive longer periods of partial submergence as compared with other crops. Likewise, a number of drought-tolerance traits of rice are the result of an altered root system architecture. Hence, the structure of the root system adapts to, both, flooding and drought. Understanding the regulatory mechanisms that control root system adaptation to extreme environments is a key task for scientists to accelerate the breeding efforts for stress-tolerant crops. This review summarizes recently identified genes and molecular mechanisms that regulate root system architecture in rice in response to drought and flooding.

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Introduction

The necessity for food production is growing with a worldwide increasing population. The World Bank pointed out that 83 million people in 45 countries were starving in 2017 (Prosekov and Ivanova 2018). A current global problem that urgently needs to be addressed is to satisfy the demand for grain yield in view of climatic changes and in view of less usable water and less cultivable land in the future. Among the approaches that are taken, improvement of crop production under adverse and extreme conditions is thought to be effective and reasonable in the present stage (Mickelbart et al. 2015). Extreme weather conditions, causing flooding and drought, are threatening crop growth, eventually resulting in loss of grain yield at harvest. Rice (*Oryza sativa* L.) is an important cereal crop that provides the main source of food for many people in Asia and Africa. Identifying the crucial traits responsible for stress resistance, and breeding rice

varieties with these traits such that plants thrive under extreme conditions, are major tasks for scientists.

Roots are indispensable for autotrophic plants. The functional root system anchors the plant, facilitates water uptake, acquisition of mineral nutrients, and engages in the formation of plant-microorganism communities in the rhizosphere (Orman-Ligeza et al. 2013). Roots are most prone to flooding conditions, and are faced with the necessity to ensure water and nutrient supply under oxygen-deficient conditions that limit ATP synthesis (Sauter 2013). The root system adapts to low oxygen and other abiotic stresses as well as to pathogenic and beneficial organisms. Root system architecture describes the three-dimensional shape and the spatial arrangement of roots in soil. The root system is made up of the primary root, lateral roots and adventitious roots (ARs). The three-dimensional root system architecture is determined by the position of the roots, root numbers, root lengths and the root

CONTACT Chen Lin ✉ stu127853@mail.uni-kiel.de

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growth angles (Rogers and Benfey 2015). The root system is regulated by both, genetic factors and environmental signals and is continuously adapted to exploit the soil for water and nutrient resources under given and oftentimes changing environmental conditions.

Substantial progress has been made in understanding the development of lateral roots and root growth regulation in the dicot model plant *Arabidopsis*. In contrast to *Arabidopsis*, the root system of cereal plants is composed mainly of ARs. Even though some physiological and molecular mechanisms that control lateral and AR development are shared, there are also root type-specific or species-specific differences that reflect the phylogenetic plant origin or the adaptation to an ecological niche. As a monocot model plant with the advantage of a relatively small-sized genome, rice is widely used in molecular-genetic studies. Several rice genomes have been sequenced to date (Wang et al. 2018) providing genomic information that help in the characterization of gene functions and in transcriptome studies. Efficient transformation systems, mutant collections and the generation of introgression lines further aid in functional gene analysis. These tools have led to the identification and functional characterization of a number of genes with a role in root development and growth in recent years (Meng et al. 2019). Nonetheless, the molecular network that regulates AR formation, growth and spatial orientation is still largely unknown. An exciting challenge in the future will be to decipher the molecular control of the root system architecture and dissect functional genes for breeders to improve crop tolerance to biotic and abiotic stress. This review focuses on our current understanding of the regulatory mechanisms and molecular players associated with AR system development in rice. In addition, ideotypes are proposed for root system architecture in response to drought and flooding conditions for the aim of further research.

Types of roots in rice system architecture

Root systems consist of embryonic and postembryonic roots (Fig. 1). Unlike many dicot plants that rely on the primary root and branching lateral roots, most cereal plants, including rice, wheat and barley, form a dense fibrous root system made up of crown roots and nodal ARs (Rebouillat et al. 2008; Coudert et al. 2010). Rice seeds germinate with a thick embryonic radicle. During seedling development, four or five crown roots

grow from the coleoptile node (Fig. 1A). These seedling roots play an important role in exploring and monitoring soil conditions (Sauter 2013). At the postseedling stage, AR primordia develop at the stem nodes to eventually form the mature rice root system. ARs are commonly classified into underground and above ground ARs. It depends on the ecotype and on the environment whether ARs are above or under ground. In general, lowland rice produces more underground ARs and few above ground ARs. Deepwater rice is adapted to grow in areas with fluctuating water levels to which they adapt through stem growth and the development of ARs from above ground stem nodes. In addition, ARs form lateral roots to enlarge the area that is explored by the root system (Fig. 1B). Lateral ARs can be categorized into large lateral and small lateral roots, that display different root lengths (Rebouillat et al. 2008). Hence, the different root types contribute to the root system architecture in rice.

Crown and adventitious root formation and growth in rice is controlled by phytohormones

Root formation and growth in rice is mediated by phytohormones. Auxin and cytokinins are essential for the *de novo* genesis of root primordia. But recent reports also describe the involvement of other hormones, such as abscisic acid (ABA) and gibberellic acid (GA), in root formation and growth.

Figure 1. Root types and schematic root system architecture in rice plants. (A) Root system of a 10-day-old rice seedling of the cultured variety Nipponbare (bar = 1 cm). (B) Scheme of a mature rice root system in soil. The root system architecture in rice is mainly composed of the radicle with lateral roots, above ground adventitious roots (AR), underground ARs and lateral ARs.

Auxin

Previous studies have extensively reported on the role of auxin on the *de novo* genesis of ARs. In plants, auxin is synthesized mainly through the highly conserved TAA/YUC pathway (Zhao 2012). Indole-3-pyruvate (IPA) is produced by tryptophan (Trp) aminotransferase of Arabidopsis (TAA) from Trp and converted to natural indole-3-acetic acid (IAA) by YUCCA flavin monooxygenases through oxidative decarboxylation (Mashiguchi et al. 2011; Won et al. 2011). Overexpression of *OsYUCCA1/OsYUC1* in rice plants results in more crown root formation (Yamamoto et al. 2007; Zhang et al. 2018). Similarly, overexpression of *OsYUC3*, *OsYUC5*, *OsYUC6*, *OsYUC7*, *OsYUC8* and *OsYUC11* promotes crown root initiation indicating that the YUCCA gene family universally regulates root formation by controlling the biosynthesis of endogenous auxin. The disruption of *TAA1* resulted in reduced crown root formation, supporting the crucial role of auxin in AR formation in rice (Zhang et al. 2018).

Rice *CROWN ROOTLESS 1/ADVENTITIOUS ROOTLESS 1* (*CRL1/ARL1*), a plant-specific *LATERAL ORGAN BOUNDARIES* (*LOB*) family member, is essential for AR initiation. It is auxin-regulated and acts downstream of auxin response factors (ARFs) (Inukai et al. 2005; Liu et al. 2005). A number of additional crown rootless mutants were identified, some of which have been functionally characterized and shown to be involved in auxin-controlled AR initiation and growth. *CRL4/OsGNOM1* is a guanine nucleotide exchange ADP-ribosylation factor that controls cycling and polar localization of the auxin efflux carrier PIN1 (Kitomi et al. 2008; Liu et al. 2009). *crl4* plants display reduced crown root and lateral root numbers together with impaired gravitropism. *CRL5*, an AP2/ERF transcription factor, is regulated by auxin through ARF transcription factors. It promotes crown root formation through inhibition of cytokinin signaling (Kitomi et al. 2011). *CRL6* encodes a protein from the large chromodomain, helicase/ATPase, and DNA-binding domain (CHD) family. Root initiation and development are under the control by *CRL6* through downregulation of *OsIAAs*, transcriptional repressors of *ARF* genes in the auxin signaling pathway (Wang et al. 2016). Although *CRL2* and *CRL3* mutants were shown to have fewer crown roots, their gene functions have yet to be elucidated (Inukai et al. 2001; Kotomi et al. 2008). The auxin efflux carrier protein *OsPIN1* mediates auxin-dependent AR emergence. In *OsPIN1* RNA interference (RNAi) plants, AR emergence is reduced,

a phenotype that is partly reverted by application of the synthetic auxin α -naphthylacetic acid (α -NAA) (Xu et al. 2005). *OsPIN1 β -galactosidase* reporter gene analysis revealed expression of *OsPIN1b* and *OsPIN1c* in growing AR primordia and local expression of *OsPIN2* in epidermal cells above AR primordia supporting the idea that polar auxin transport contributes to AR growth and possibly to death of epidermal cells that cover AR primordia which facilitates AR emergence (Steffens and Sauter 2005; Lin and Sauter 2019).

The Ca^{2+} -independent Ser/Thr kinase gene *OsRPK1* functions as a negative regulator of AR development by inhibiting polar auxin transport via PIN proteins. Knockdown of *OsRPK1* promoted AR initiation (Zou et al. 2014). The *Aux/IAA* gene *OsIAA23* is required for the auxin-mediated maintenance of the quiescent center in postembryonic roots. *Osiaa23* mutants have fewer crown and lateral roots compared with the wild-type (Jun et al. 2011). *NARROW LEAF 1* (*NAL1*) encodes a putative trypsin-like serine/cysteine protease. Loss of *NAL1* results in a decreased number of ARs, a phenotype that was rescued by exogenous auxin, suggesting that *NAL1* also controls AR growth through the auxin signaling pathway as was shown for several crown rootless mutants (Cho et al. 2013). Moreover, *OsCAND1*, that is responsible for maintaining the G2/M cell cycle transition, regulates crown root formation through the control of the endogenous auxin level. *Oscand1* shows an abnormal crown root formation that could be partly compensated by exogenous auxin (Wang et al. 2011). Additionally, a point mutation of *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 3* (*OsSPL3*) repressed the auxin signaling pathway, resulting in a rootless phenotype further supporting the conclusion that auxin plays a crucial role in AR formation in rice (Shao et al. 2019).

Cytokinins

Growing evidence demonstrates the involvement of cytokinins in AR emergence and growth in rice. Cytokinin receptors activate two types of primary response regulators (RRs), designated type-A and type-B RRs. Type-A RRs act as negative regulators whereas type-B RRs have activating activity. In the presence of cytokinin, type-A RR genes display distinct expression patterns suggestive of specific functions of OsRR proteins in response to cytokinin (Gao et al. 2014). Rice type-A RR6 negatively regulates shoot and root growth. Overexpression of *RR6* results in a severe rootless phenotype (Hirose et al. 2007). *OsCKX4*, a cytokinin oxidase/dehydrogenase

(CKX) family gene, is targeted by auxin response factor OsARF25 and the type-A response regulators OsRR2 and OsRR3. Overexpression of *OsCKX4* in rice promotes crown root formation (Gao et al. 2014). Finally, *CRL5* is a positive regulator of crown root formation that acts by repressing cytokinin signaling (Kitomi et al. 2011).

The *WUSCHEL*-related homeobox gene *WOX11* is expressed in emerging ARs. It maintains cell division in the root apical meristem. In rice, *wox11* knockout plants and *wox11*-RNAi lines show reduced crown root formation, whereas overexpression of *WOX11* results in ectopic AR growth, indicating that *WOX11* is essential for the development of crown root formation in rice (Zhao et al. 2009). The AP2/ERF protein ERF3 interacts with *WOX11* and co-regulates crown root development. Knockdown of *ERF3* in a *wox11* mutant background showed a more severe rootless phenotype whereas overexpression of *ERF3* partially rescued the *wox11* phenotype. Both, *WOX11* and *ERF3* target the type-A *RR2* gene that regulates crown root initiation in response to cytokinin (Zhao et al. 2015). *WOX11* also recruits an ADA2-GCN5 histone acetyltransferase module to regulate root-specific genes involved in cell division and root meristem activity (Zhou et al. 2017) suggesting that AR formation is also regulated at the epigenetic level. Additional evidence suggests that the TAA/YUC pathway functions together with *WOX11*, indicating that auxin and cytokinin signaling pathways merge at the level of *WOX11* (Zhao et al. 2009; Zhang et al. 2018).

Ethylene and abscisic acid

Unlike auxin and cytokinin, that are involved in the *de novo* genesis of rice roots, ethylene represses radicle root growth, and was shown to promote AR emergence and growth in rice. The ethylene signaling pathway of rice remained unexplored for a long time due to the lack of mutants (Rzewuski and Sauter 2008). The transcription factor *ETHYLENE INSENSITIVE 3* (*EIN3*) is a key regulator of ethylene signaling in Arabidopsis. The homologous gene *OsEIL1* of rice, when expressed in the Arabidopsis *ein3* mutant background, partially compensated the short-root phenotype (Mao et al. 2006) suggesting that key signaling elements are conserved between dicot and monocot plants. Nonetheless, specific regulatory mechanisms in ethylene signaling of root development need yet to be elucidated. The ethylene response factor gene *OsERF2* regulates the levels of ethylene and abscisic

acid (ABA) and is essential for embryonic root growth (Xiao et al. 2016). In recent years, a number of rice mutants were identified that develop more ARs (Yin et al. 2018). These mutants were termed *mao hu zi* (*mhz*), which means 'cat whiskers' (Chen et al. 2018). Several of the corresponding *mhz* genes were identified through map-based cloning and their functions were studied (Fig. 4A). *MHZ7* is the rice homolog of Arabidopsis *EIN2* (Merchante et al. 2013; Li et al. 2015). *MHZ7:GUS* reporter analysis revealed expression of *MHZ7* in both the embryonic root and in ARs. Overexpression of *MHZ7* led to a short, twisted radicle in rice seedlings (Ma et al. 2013). *MHZ6* encodes a homolog of Arabidopsis *EIN1*. Loss of *MHZ6* results in roots that are insensitive to ethylene (Yang et al. 2015). *MHZ7* and *MHZ6* are considered central components in the ethylene signaling pathway based on the crucial role of orthologous genes *EIN2* and *EIN1* in Arabidopsis. *MHZ3* is an endoplasmic reticulum-localized membrane protein that is required for the stabilization of *MHZ7* (Ma et al. 2018). *MHZ5* encodes a carotenoid isomerase involved in carotenoid biosynthesis. *MHZ5* gene expression was induced by ethylene and results in ABA accumulation in the root, which, in turn, inhibits root growth. *MHZ4* is homologous to *ABA4* of Arabidopsis, that was previously shown to regulate the interplay between ethylene and ABA. Overexpression of *MHZ4* enhanced the ethylene sensitivity of seedling roots and increased the endogenous ABA level. Disruption of *MHZ4* induced AR formation at the nodes (Ma et al. 2014). ABA promotes expression of *MAIF1* that codes for an F-box domain protein localized at the plasma membrane and in the nucleus. Ectopic overexpression of *MAIF1* enhanced root growth (Yan et al. 2011). Taken together, these findings suggest that *MHZ4* and *MHZ5* mediate the interaction between ethylene and ABA pathways in regulating root growth in rice (Yin et al. 2015). The mutant analysis revealed molecular components of the ethylene-ABA crosstalk that was previously described at the physiological level (Steffens et al. 2006).

Gibberellic acid and salicylic acid

The hormonal network that regulates AR development and growth in rice includes additional hormones but the molecular mechanisms of their activities have not been exhaustively studied. The AP2/ERF transcription factor *OsSHB* targets the gene *KS1*, which encodes the entkaurene synthase of gibberellic acid (GA) biosynthesis

controlling proliferation and elongation of root meristem cells. *Osshb* knockout plants have fewer and shorter roots compared with the wildtype (Li et al. 2015) supporting previous physiological studies that revealed enhanced AR growth in the presence of GA (Steffens et al. 2006). The 3-hydroxyacyl-CoA dehydrogenase *ABNORMAL INFLORESCENCE MERISTEMI 1* (*AIM1*) controls root mitotic activity in rice by promotion of salicylic acid (SA) synthesis and repression of redox-related genes and of genes involved in scavenging of reactive oxygen species (ROS), with elevated ROS levels as a result (Xu et al. 2017).

The growth angle of rice ARs is determined by genetic factors and by the environment

Root system architecture is determined by the number and position of roots, the growth rates and the root growth angles. The functional root system adjusts these parameters to optimize exploitation of the soil and to ensure uptake of nutrients and water in an inhomogeneous soil substrate or when soil parameters change. Analysis of root systems in their natural underground environment is difficult. Non-destructive 3D-imaging techniques such as Magnetic Resonance Imaging (MRI) and X-ray Computer Tomography (CT) elegantly address this issue and allow visualization of entire root systems in soil with a high resolution (Metzner et al. 2015). In general, roots grow toward higher water potential, nutrients and oxygenated areas. By contrast to the soil-borne root system, nodal ARs that emerge upon flooding grow in an aquatic environment where other environmental cues become important.

One such factor is light, which regulates growth of above-ground ARs and of roots that grow at the soil surface. In rice, above-ground ARs grow upward in the dark whereas in the light, ARs grow downward (Lin and Sauter 2018). The AR growth angle is determined by far red, red and blue light revealing negative phototropism controlled by phytochrome (Pr and Pfr) and blue light signaling likely through phototropin (Lin and Sauter 2018). Roots are sensitive to gravity with primary roots displaying positive gravitropism whereas lateral and ARs grow at an angle that is genetically determined, the gravitropic setpoint angle, and also subject to regulation by environmental cues (Baldwin et al. 2013; Rogers and Benfey 2015). Non-vertical root

growth is the result of differential growth rates at opposite sides caused by an asymmetric auxin distribution across the root tip. *DEEPER ROOTING 1* (*DRO1*) is an auxin-regulated gene that promotes a more vertical root growth angle resulting in an overall deeper root system. *DRO1* is expressed in the cell elongation zone at the root tip and is responsive to gravity (Uga et al. 2013).

It is well established that polar auxin transport contributes to asymmetric auxin distribution in the root (Petrasek and Friml 2009; Adamowski and Friml 2015). PIN-formed (PIN) proteins are auxin efflux carriers localized at the plasma membrane that are responsible for auxin efflux from the cell. PIN efflux carriers are key determinants of directed auxin transport in the plant and for generating auxin gradients. In Arabidopsis, PIN1 drives acropetal auxin transport in the central cylinder of roots. PIN3, PIN4 and PIN7 redirect the auxin flux in the root cap to the peripheral cell layers while PIN2 directs the basipetal auxin transport toward the root base. PIN5, PIN6 and PIN8 are located at the endoplasmic reticulum and their functions in roots are still largely unknown (Adamowski and Friml 2015). In rice, at least 12 PIN proteins have been predicted based on homologies to Arabidopsis PINs (Fig. 2A). OsPIN1a-d are the rice homologs of AtPIN1 and OsPIN2 is homologous to AtPIN2. AtPIN5 has 3 homologs in rice, OsPIN5a, OsPIN5b and OsPIN5c. OsPIN10a and OsPIN10b are most related to PIN3, PIN4 and PIN7. So far, the functions of OsPINs in determining the root growth angle is largely unclear. The auxin flux mediated by PIN proteins in the rice root can be predicted based on these homologies and the functional characterization of PINs in Arabidopsis (Fig. 2B). OsPINs show different expression patterns in the radicle and in above-ground ARs (Wang et al. 2009; Lin and Sauter 2019). Despite the fact that AR growth direction is largely determined by light, light did not much alter *PIN* gene expression in ARs. It is conceivable that OsPIN localization and activities are regulated through posttranscriptional mechanisms (Eysholdt-Derzso and Sauter 2017; Lin and Sauter 2019). The *OsPIN2* mutant exhibited decreased sensitivity to gravity and showed an increased root growth angle (Wang et al. 2018) suggesting that the gravitropic setpoint angle is in part determined by polar auxin transport via OsPIN2.

In addition to efflux carriers, the auxin influx carrier gene *OsAUX1* also positively regulates the root growth

A **B**

Figure 2. Phylogenetic relationship of PIN proteins in Arabidopsis and rice and predicted polar auxin transport (PAT) in the rice root. (A) Phylogenetic analysis of PIN family members in rice and Arabidopsis. A multiple sequence alignment was carried out with Clustal Omega and a phylogenetic tree was generated using Treeview; bar = 0.1. (B) Predicted schematic PAT through rice PIN proteins.

angle. *Osaux1* plants have a shallower root system than wild type. In addition, *OsAUX1* promotes root hair elongation thereby improving the phosphate acquisition in low phosphate conditions. *OsAUX1* plays an important role in auxin transport from the root apex to the differentiation zone (Giri et al. 2018). In summary, investigations of the molecular mechanisms that control the root growth angle in rice have just begun, which holds true also for other cereal crops. Understanding the regulatory network that controls the root growth angle will be a prime task for future research and will help design cereal root systems adapted to a challenging environment.

Changes in root system architecture in response to drought

Drought causes grain yield loss due to water deficit in the plant (Atkinson and Urwin 2012). Severe or long-lasting drought renders the root system damaged or dysfunctional which limits the uptake of water and

nutrients or makes it impossible (Rogers and Benfey 2015). For the benefit of the plant and with regard to agricultural yield, an adjustable root system that confers drought tolerance is a desirable trait.

A number of transcription factors have been studied that enhance plant survival under drought conditions. Genes of the NAC domain family of rice have received significant interest due to their specific roles in drought adaptation of the root system (Ooka et al. 2003). Plants that express *NAC9* under a root-specific promoter, acquire thicker roots with an enlarged stele and large aerenchyma. Several genes related to root morphogenesis as well as cell elongation and lignin and suberin biosynthesis for walls of the rhizodermis were found to be upregulated in the root of *NAC9* overexpressed transgenic plants through microarray analysis (Redillas et al. 2012). The morphological changes might account for the improved grain yield under drought conditions. Similarly, *OsNAC10* expression driven by a root-specific promoter caused an increase in root volume, length, dry weight, and diameter together with enhanced

grain yield, both, in non-stressed and drought conditions (Jeong et al. 2010). *SNAC1* is a stress-related NAC family member, that is involved in the adaptation to drought and salt stress. When overexpressed in cotton (*disambiguation*), *SNAC1* produced more roots compared with wildtype plants (Liu et al. 2014). Similarly, *NAC045* also confers drought tolerance in rice plants (Zheng et al. 2009), even though the root phenotypes have not been described yet. In summary, NACs confer drought tolerance mainly by increasing the root volume, both, in length and diameter, and by changing the root anatomy. In addition, *RSOsPR10*, a rice root-specific pathogenesis-related protein, also enhances drought resistance in plants by enhancing the root mass (Takeuchi et al. 2016). *WOX11* mediates drought resistance in plants by controlling the number of crown roots, lateral roots and root hairs (Cheng et al., 2016). In contrast, *DEEPER ROOTING 1 (DRO1)* increases the root angle allowing the plant to explore water resources in deeper soil layers (Uga et al. 2013; Fig. 3A).

It is well supported that endogenous ABA levels increase in response to drought (Kuromori et al. 2018). ABA alleviates drought stress mainly through enhanced net photosynthesis, stomatal closure and the resulting decreased transpiration rate (Teng et al. 2014). On the other hand, ABA inhibits root growth and hampers water transport. ABA synthesis is mainly detected in young root tips but not in mature roots, which is thought to be an early response to drought (Schachtman and Goodger 2008). However, growing evidence suggests that a high ABA content in long-lasting droughts restricts the root growth, which is not beneficial for plants (Shi et al. 2015).

In general, a deep and thick root system confers higher resistance to drought. Thick roots have a larger diameter that enhances the penetration ability in soil allowing faster and deeper growth of roots. In addition, thick roots with additional xylem strands can transport more water, which is beneficial for water uptake and will reduce axial water stress (Yambao et al. 1992). It was estimated that xylem with a pit anatomy is less leaky and transports water more efficiently (Pandey et al. 2015).

During plant breeding, a number of advantageous abiotic stress tolerance genes were lost. It is however possible to identify the respective traits through QTL mapping in the wild rice species. Deeper root is a good example providing the potential for improved rice resistance to drought. The challenge ahead is thus to

identify the genes that improve drought tolerance and minimize crop loss.

Adaptive role of rice root system architecture upon flooding

Flooding and soil water-logging are threatening many crops and weather extremes with severe floods are increasing worldwide (Mustroph 2018). When flooded, the root system is prone to oxygen shortage which limits its uptake and transport capacity for nutrients and water. The maintenance of a functional root system is a prerequisite for plants to survive flooding (Sauter 2013). Several plant species including rice (Lorbiecke and Sauter 1999), tomato (*Solanum lycopersicum*) and tamarack (*Larix laricina*) (Calvo-Polanco et al. 2012) developed an adaptive strategy. They replace the damaged roots by ARs through *de novo* formation or by promoting emergence of existing AR primordia. In rice, ARs are formed at each node during nodal development and remain buried until triggered to emerge by flooding. In tamarack, long-term submergence results in the complete loss of the original roots which are gradually replaced by ARs (Calvo-Polanco et al. 2012). Nodal ARs provide the advantage of a reduced distance for O₂ transport from the shoot. The porosity in flooding-induced ARs is higher compared with unflooded roots due to aerenchyma formation (Webb and Jackson 1986; Laan et al. 1989; Drew et al. 2000; Argus et al. 2015). Furthermore, ARs tend to float at or near the water surface which facilitates uptake of atmospheric oxygen (Dawood et al. 2016). In several plants, including *Tecticornia pergranulata*, aquatic ARs develop chloroplasts and are photosynthetically active to partially compensate for the decreased rate of photosynthesis under water with O₂ release as a side effect (Rich et al. 2008). Deepwater rice, adapted to long-lasting floods, develops more nodes than lowland rice which allows deepwater rice plants to form more ARs. When floods recede and deepwater rice stems bend to the ground, ARs can grow into the soil thereby avoiding root desiccation and providing anchorage for the plant (Fig. 3A-B).

In rice, induction of AR emergence is triggered by ethylene that gets trapped in the flooded plant (Fig. 4B). Ethylene promotes cell cycle activity at the nodes (Lorbiecke and Sauter 1999), indicating that AR growth is distinctly regulated compared to primary or lateral root growth that is inhibited by ethylene. Inhibition

Figure 3. Root systems during drought and flooding. (A) Scheme of a shallow and a deep root system in drought or flooding conditions. (B) Adventitious root growth in 3-month-old Nipponbare plants grown under non-flooded conditions or exposed to partial submergence for 15 days.

of ethylene perception by 1-methylcyclopropene (1-MCP) abolished AR emergence revealing a requirement for ethylene signaling (Lin and Sauter 2018). The AR primordium is covered by the nodal epidermis that acts as a physical barrier (Sauter 2013). Programmed death of epidermal cells above AR primordia occurs prior to AR emergence which weakens the epidermal barrier and protects the AR meristem from injury (Steffens and

Figure 4. Model of ethylene signaling during submergence. (A) The ethylene signaling pathway of rice based on the analysis of *mao hu zi* (*mhz*) mutants. (B) Ethylene signaling of adventitious root growth and epidermal cell death (PCD) in rice. A nodal cross section was stained with toluidine to visualize the root primordium.

Sauter 2005). Epidermal cell death and AR growth are induced by ethylene, promoted by GA and inhibited by ABA (Steffens et al. 2006) indicating that the interaction and balance of these phytohormones coordinates growth and death in a timely and spatially coordinated manner. Hydrogen peroxide produced by NADPH oxidase at the plasma membrane acts downstream of ethylene in cell death induction. In addition, reduced expression of the ROS scavenger gene *METALLOTHIONEIN*

2B (*MT2b*) enhances the accumulation of reactive oxygen species and promotes cell death (Steffens and Sauter 2009). The spatial control that limits epidermal cell death to sites where ARs emerge is provided by a mechanical signal coming from the growing AR (Steffens et al. 2012). Both, mechanical force and ethylene signaling via reactive oxygen species are required to trigger the death of epidermal cells.

In rice, ethylene is a positive regulator of AR growth. ARs are crucial for plant survival of submergence. While the blueprint for the ethylene signaling pathway in rice has been established (Fig. 4A) the distinct molecular mechanisms that drive AR growth still need to be uncovered. More so, the majority of studies carried out in rice to date focused on seedlings rather than on mature plants where the adaptive root systems may be controlled differently. And finally, different rice cultivars have developed different survival strategies with an escape response in deepwater rice cultivars and a quiescence response in lowland rice (Voeseinek and Bailey-Serres 2009). It is conceivable that different strategies exist in the development of the AR system. To test this hypothesis, a systematic comparison of root system architecture in different rice types will have to be done.

Conclusion

Root system architecture in rice is regulated developmentally and by environmental cues. Both regulatory venues rely on phytohormones as key signals. To date, a few genes that are functionally associated with rice root development have been identified and characterized, but the regulatory network that integrates endogenous and exogenous signals still needs to be uncovered. An improved understanding of the molecular mechanisms that control root system development and determine root system architecture will help accelerate breeding of plants with a root system that is optimized to cope with drought and floods to ensure stable crop production.

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